To Bill Brown with best regards from Laurie Burnham
6820

Survey of Social Insects in the Fossil Record

BY LAURIE BURNHAM

Reprinted from PSYCHE, Vol. 85, No. 1, March 1978
pages 85-133

6820

Reprinted from PSYCHE, Vol. 85, No. 1, March 1978

SURVEY OF SOCIAL INSECTS IN THE FOSSIL RECORD*

By Laurie Burnham
Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138, U.S.A.

Biologists have long been intrigued by the complex social systems of various insects. Despite a voluminous literature dealing with the evolution of these systems, immense gaps remain in our understanding of insect sociality. Several theories have been proposed to explain the evolution of social behavior in certain groups of insects (e.g., Hamilton, 1964), but none consider this problem with respect to geological time. The present paper does so by examining the fossil record for clues not only on the antiquity of sociality, but also on the nature of these early social insects. Included in this survey are those insects recognized as eusocial: the Isoptera, and three superfamilies of the Hymenoptera: Vespoidea, Formicoidea, and Apoidea.

ISOPTERA

The termites are remarkable in two regards: 1) as a group, they are fully eusocial, exhibiting a wide range of behavioral modifications and sophistications, and 2) their record in the geological past, although sparse, is highly indicative of an Early Mesozoic origin. This latter point is of particular significance if one considers sociality among insects as a pinnacle of evolutionary success. Wilson (1971, p. 1) states that "[insect societies] best exemplify the full sweep of ascending levels of organization, from molecule to society." The possibility that termites evolved a social organization as far back in geological time as the Jurassic (roughly 190 million years ago) is of great interest, particularly when attempting to draw parallels with the evolution of sociality in the Hymenoptera, a group phylogenetically very remote from the termites.

Manuscript received by the editor July 7, 1978.

Five of the six families[1] of termites recognized by Emerson (1955) have a fossil record extending at least as far back as the Tertiary. In 1967, *Cretatermes carpenteri* (Hodotermitidae) was found in an Upper Cretaceous deposit in Labrador (Fig. 1), a discovery which immediately placed the origin of the Isoptera no later than the Mesozoic — an extension of 45 million years from previously known specimens. In addition, the advanced phylogenetic position of *Cretatermes* provides evidence for a much earlier origin of the order than has formerly been recognized (Emerson, 1967).

An examination of various fossil localities reveals a widespread termite fauna during the Tertiary Period (Table 1). The Termitidae are found in Miocene deposits of California and Germany; the Rhinotermitidae, Hodotermitidae, and Kalotermitidae are found at various Tertiary deposits throughout the United States and Europe; and the Mastotermitidae have the most widespread Cenozoic distribution of all, having been found at localities in the United States, Europe, South America, and Australia. This latter finding is highly intriguing because the family Mastotermitidae today has but one species, *Mastotermes darwiniensis,* which is restricted to northern Australia.[2] Emerson (1955) postulates that this widespread

[1]The sixth family is the Serritermitidae — an aberrant taxon known from only one species.

[2]A look at past climatic shifts provides additional insight into the redistribution of the termites, particularly with respect to the Mastotermitidae, now solely restricted to Australia. Reconstructions of paleo-climatic patterns may be made fairly accurately on the basis of floral analyses (Reid and Chandler, 1933). The presence of *Sequoia* stumps in the Florissant Shales of Colorado provides evidence for warmer temperatures during the Oligocene (Emerson, 1969). Tiffney (1977) postulates on the basis of fossil angiosperm assemblages that temperatures in New England during the Oligocene were much more equable than at present — the temperatures ranging from 26° C to 9° C in contrast to today's 21° C to −10° C. Furthermore, extended frosts and hard freezes were unknown. In the more tropical climate of the Oligocene, colony activities were presumably carried out year round in a relatively warm, moist environment, explaining the widespread distribution of the Mastotermitidae during the Lower to Middle Tertiary. By the Late Miocene or Early Pliocene, the earth's climate began shifting towards cooler temperatures with the rising level of the continental land masses and increasingly large polar ice caps. My hypothesis is that, unable to adapt to an increasingly colder climate, and possibly to a concomitant change in predator pressures, the Mastotermitidae began to die out during the Tertiary. And, because at this time the Termitidae were undergoing tremendously successful radiation in Africa and South America, the Mastotermitidae became geographically restricted to northern Australia, represented today by only one relict species, *Mastotermes darwiniensis.*

Figure 1. *Cretatermes carpenteri* Emerson from lower part of Upper Cretaceous of Labrador. Note humeral suture at wing base. Original photograph of holotype in Princeton Museum. Length of wing, 7.5 mm.

geographical distribution provides strong evidence to support a Mesozoic origin of the order. He argues (1975) that the breakup of the united land mass Pangaea in the Permian or Lower Triassic must have occurred subsequently to the origin of the Isoptera to explain their distribution in the southern and northern continental land masses and that all five families must have been present in the Late Mesozoic to explain their diversity and distribution by the Tertiary.

In 1971 he looked at a variety of primitive and derived characters of each family and analyzed the geographical distribution of the groups, using plate tectonics to provide the following estimates on the geological origin of the families:

Mastotermitidae — possibly Early Mesozoic.

Hodotermitidae — Triassic, or Early Jurassic before the breakup of southern continents.

Kalotermitidae — mid-Jurassic, or Lower Cretaceous, before the separation of Africa and South America.

Rhinotermitidae — Late Jurassic, Early Cretaceous.

Termitidae — Cretaceous.

Because termites are such poor fliers and do not mate until the adults have cast their wings, he considers water gaps of more than 50 miles capable of preventing termite dispersal.

While I am supportive of the theory that places great importance on the role of a unified land mass in animal dispersal, I do not agree that this can effectively be used to date the origin of the Isoptera.

TABLE 1 ISOPTERA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Hodotermitidae		
**Cretatermes carpenteri* Emerson	Labrador, Canada	Emerson, 1967
EOCENE		
Mastotermitidae		
**Blattotermes wheeleri* Collins	Tennessee, U.S.A.	Emerson, 1965
**Idomastotermes mysticus* Häupt	Geiseltal, Germany	Emerson, 1965
Kalotermitidae		
Neotermes grassei Piton	Menat, France	Emerson, 1969
Hodotermitidae		
Termopsis mallaszi Pongracz	Hungary	Snyder, 1949
OLIGOCENE		
Mastotermitidae		
**Miotermes insignis* (Heer)	Oeningen, Germany	Emerson, 1965
**Miotermes spectabilis* (Heer)	Oeningen, Germany	Emerson, 1965
Mastotermes bournemouthensis von Rosen	England	Emerson, 1965
Mastotermes heeri (Göppert)	Schlesien, Germany	Emerson, 1965
Mastotermes batheri von Rosen	England	Emerson, 1965
Kalotermitidae		
**Prokalotermes hageni* (Scudder)	Florissant, Colorado	Emerson, 1969
**Electrotermes giradi* (Giebel)	Baltic Amber	Emerson, 1969
**Electrotermes affinis* (Hagen)	Baltic Amber	Emerson, 1969
Kalotermes rhenanus Hagen	Rott, Germany	Emerson, 1969
**Eotermes grandaeva* Statz	Rott, Germany	Emerson, 1969
**Proelectrotermes berendti* (Pictet)	Baltic Amber	Emerson, 1969

Hodotermitidae		
Archotermopsis tornquisti von Rosen	Baltic Amber	Snyder, 1949
Termopsis bremii Heer	Baltic Amber	Snyder, 1949
**Parotermes insignis* Scudder	Florissant, Colorado	Snyder, 1949
**Parotermes scudderi* Cockerell	Florissant, Colorado	Cockerell, 1913
**Ulmeriella bauckhorni* Meunier	Rott, Germany	Emerson, 1968
**Ulmeriella cockerelli* Martynov	Siberia, U.S.S.R.	Emerson, 1968
Rhinotermitidae		
**Reticulitermes minimus* (Snyder)	Baltic Amber	Emerson, 1971
Reticulitermes fossarum (Scudder)	Florissant, Colorado	Emerson, 1971
Reticulitermes antiquus (Germar)	Baltic Amber	Emerson, 1971
Reticulitermes creedei Snyder	Creede, Colorado	Emerson, 1971
**Parastylotermes robustus* (Rosen)	Baltic Amber	Emerson, 1971
MIOCENE		
Mastotermitidae		
**Spargotermes costalimai* Emerson	Brazil	Emerson, 1965
Mastotermes vetustus Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes minor Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes haidingeri (Heer)	Radoboj, Croatia	Emerson, 1965
Mastotermes croaticus von Rosen	Radoboj, Croatia	Emerson, 1965
**Miotermes procerus* (Heer)	Radoboj, Croatia	Emerson, 1965
**Miotermes randeckenensis* von Rosen	Württemberg, Germany	Emerson, 1965
**Pliotermes hungaricus* Pongracz	Radoboj, Croatia	Emerson, 1965
Kalotermitidae		
Cryptotermes ryshkoffi Pierce	Calico, California	Emerson, 1969
Kalotermes swinhoei (Cockerell)	Burma	Emerson, 1969
Kalotermes tristis (Cockerell)	Burma	Emerson, 1969
Kalotermes nigritus Snyder	Chiapas, Mexico	Snyder, 1960

TABLE 1. (CONCLUDED)

Geological Age	Locality	References
MIOCENE (continued)		
Hodotermitidae		
**Ulmeriella latahensis* Snyder	Latah, Washington	Emerson, 1968
**Ulmeriella martynovi* Zeuner	Biebrich, Germany	Emerson, 1968
Rhinotermitidae		
Heterotermes primaevus Snyder	Chiapas, Mexico	Emerson, 1971
Reticulitermes hartungi (Heer)	Radoboj, Croatia	Emerson, 1971
Reticulitermes laurae Pierce	Calico, California	Emerson, 1971
**Parastylotermes calico* Pierce	Calico, California	Emerson, 1971
**Parastylotermes washingtonensis* (Snyder)	Latah, Washington	Emerson, 1971
Termitidae		
Gnathamitermes magnoculus rousei Pierce	Calico, California	Pierce, 1958
Macrotermes pristinus (Charpentier)	Radoboj, Croatia	Snyder, 1949

*Extinct genera.

Simpson (1952) has made some insightful remarks on the matter. He contests the premise that if a given group of organisms requires a land connection, then disjunctive areas occupied by the group must have been once connected by continuous land. His contention is that there is no group of organisms that cannot be dispersed over water. Given a probability of only one chance in a million that an organism can cross a stretch of water, when geological time is considered the chance that the event will actually take place (over tens of millions of years) becomes significantly greater. It is further argued that successful colonization is dependent on successful invasion and the ability of the intruder to compete with existing species. Chances for survival are much higher when there are numerous, simultaneous arrivals of individuals.

In my opinion, the termites support such reasoning, and this can be argued in several ways. Firstly, termites are relatively light-bodied, winged insects. Studies by Simberloff and Wilson (1969) and Glick (1933) on the repopulation of an island by wind transported insects strongly support the possibility that termites are capable of being carried considerable distances in the upper atmosphere. Furthermore, because termites swarm in such large numbers prior to reproduction, a reasonable possibility exists that they will be dispersed to a new habitat as either a group or at least as a male/female pair. A wind current strong enough to blow one individual into the upper atmosphere should be equally capable of carrying multiple individuals, and, according to windflow, of transporting them in the same directional pathway.

Secondly, termites are ideally suited to dispersal over large bodies of water via floating logs. The more primitive families construct their extensive nesting colonies in wood and logs; as a consequence, it is entirely plausible that a dead tree falling into a body of circulating water could be carried extended distances. Furthermore, this mode of transportation provides the termites with a source of food during their sojourn, and travel *en masse* obviates the problems of reproduction upon arrival. In addition, as Simpson points out, the larger the number of individuals, the more likely it is that they will be successful competitors in the new habitat. I am not presenting this as evidence that the termites did not evolve while the earth's land masses were still contiguous, but am merely pointing out the problems in arguing that land dispersal was essential for termites.

The Isoptera exhibit strong affinities to the Blattodea; evidence linking the two groups to a common ancestor is well marked between the Mastotermitidae, an archaic termite family, and the Cryptocercidae, a family of generalized cockroaches. This theory of common ancestry is supported by several comparative morphological and behavioral studies (Emerson, 1965; McKittrick, 1965; Ahmad, 1950; Cleveland, 1934; Hill, 1925). McKittrick (1965) goes so far as to incorporate both groups into the Dictyoptera, an order which also includes the Mantodea. The gut fauna, female genitalic structures, anal expansion of the hind wing, morphology of the proventriculus, and deposition of eggs in ootheca-like masses are much alike in *Mastotermes* and *Cryptocercus*. Furthermore, both groups inhabit similar habitats. As a consequence, termites have often been referred to as merely social cockroaches. This degree of relatedness becomes immediately interesting in view of the extensive geological record of the cockroaches.

Fossil cockroaches are first found in deposits from the Upper Carboniferous, which makes them among the oldest insects known. Furthermore, they comprise 80 percent of the fossil insect fauna during that period (Carpenter, 1930) — an indication that they have not only existed, but have flourished, for three hundred million years. If the similarities between termites and cockroaches are indeed the result of monophyletic, rather than convergent or parallel evolution, one might speculate on a much earlier origin for the Isoptera than is shown by the fossil record.

McKittrick (1965) admits that the flagellate gut fauna essential for cellulose digestion in both groups may have arisen independently in each; however, she believes that the similarities in two important morphological characters, the female genitalia and the dental belt of the proventriculus, represent primitive characters and are therefore indicative of a common origin for *Mastotermes* and *Cryptocercus*. On the other hand, Tillyard (1926, 1936), Cleveland (1934), Imms (1919), Carpenter (personal communication), among others, believe that the termites were derived from more ancient stock and may have evolved during the Late Paleozoic. Hamilton (1978) supports the view that social termites arose from "roach-like ancestors" in the habitat of dead phloem, and suggests that the invasion of *Cryptocercus* into the same type of habitat was independent of the ancestral termite. The possibility of termite "evolu-

tion under bark" seems immensely feasible; not only is isolation (and, hence, inbreeding) possible, but selective pressures leading to dependence on a cellulose diet would also be high. It seems an excellent explanation for the early separation of the termites and cockroaches from a common protorthopteran (protoblattoid) ancestor as long ago as the Late Paleozoic. More definite conclusions on the origin of the Isoptera must wait until termites or termite-like insects have been found in pre-Cretaceous strata.

HYMENOPTERA

The Hymenoptera belong to the major subdivision of the Insecta known as the Endopterygota. There are no clues elucidating the nature or precise age of the earliest endopterygote insects, but the fossil record does provide insight into the history of the group as a whole. Representatives of two endopterygote orders, Neuroptera and Mecoptera, are found as far back as the Early Permian, some 280 million years ago. This occurrence suggests an origin of the Endopterygota approximately 100 million years after the origin of the true insects.[3]

The earliest known Hymenoptera have been found in Triassic beds of Central Asia (Rasnitsyn, 1964) and Australia (Riek, 1955). These fossils establish a minimum age for the order of about 220 million years. All the specimens known from this period belong to the suborder Symphyta, and surprisingly enough belong to the existing family Xyelidae.

A major advance in the evolution of the Hymenoptera occurred with the development of a constriction between the first and second abdominal segments; this presumably had the selective advantage of increasing the flexibility of the abdomen, important for both oviposition and defense. Hymenoptera which possess this adaptation, a diagnostic character of the suborder Apocrita, are first known from Upper Jurassic deposits of Central Asia (Rasnitsyn, 1975, 1977). These specimens have been assigned to the more primitive division of the Apocrita known as the Terebrantia or

[3]The oldest known insects, found in Upper Carboniferous deposits, comprise 11 orders and include the Apterygota (Thysanura), Paleoptera and Exopterygota. It should be noted that here the use of the term insect does not include the Collembola, Protura or Diplura.

Parasitica; the other division within this suborder is the Aculeata.[4] Members of the latter are characterized by modifications of the ovipositor that have enabled its use not only for oviposition, but also as a transport vessel for defensive and prey-paralyzing compounds. This structure unquestionably plays an important role in colony defense and might provide an explanation for the restriction of eusociality within the Hymenoptera to the Aculeata.

The oldest known aculeate hymenopteron, *Cretavus sibericus,* was discovered in an Upper Cretaceous (Cenomanian) deposit in Siberia in 1957. Although placed by Sharov (1962) in an extinct superfamily Cretavidea, related to the Scolioidea, it has recently been transferred to the existing family Mutillidae by Rasnitsyn (1977, p. 109). Since 1967, species representing 10 families and 19 genera of aculeate Hymenoptera have been found in Upper Cretaceous deposits in Central Asia (Rasnitsyn, 1977) (Table 2). Evans (1966) believes that such diversity by the Late Cretaceous is indicative of an earlier origin and postulates that the group may have evolved during the Jurassic. However, it must be pointed out that the Cretaceous is one of the longer periods in the earth's history, having a duration of roughly 70 million years, and may have been of sufficient length to account for such diversification.

VESPOIDEA

Included in this group are the three families considered to be "true wasps": The Masaridae and Eumenidae, both of which are solitary, and the Vespidae, where one finds behavioral modifications ranging from subsocial to highly advanced eusocial (Richards, 1953, 1971). It is the Vespidae, by virtue of their sociality, with which I am primarily concerned in this paper.

There are many gaps in our record of the early social wasps and of the Vespoidea in general. Most striking, perhaps, about the fossil record of the wasps is their lack of representation (see Table 3). The

[4]The classification of the Aculeata has recently undergone a major revision by D. J. Brothers (1975), in which the seven previously recognized superfamilies (Bethyloidea, Scolioidea, Pompiloidea, Formicoidea, Vespoidea, Sphecoidea, and Apoidea) are now combined into three: the Bethyloidea, Sphecoidea (subdivided into the Spheciformes and Apiformes), and Vespoidea (subdivided into the Vespiformes and Formiciformes). However, since this revised classification has not been generally accepted in its entirety, I am employing here the more conventional classification (*sensu* Riek, 1970; Richards, 1971).

Table 2. Genera of aculeate Hymenoptera known from Cretaceous deposits (based on Rasnitsyn, 1977, and Evans, 1973). All genera are extinct.

SCOLIOIDEA		
Mutillidae	*Cretavus*	Sharov, 1962; Rasnitsyn, 1977
?SCOLIOIDEA		
Scolioidae	*Oryctopterus*	Rasnitsyn, 1977
Angarosphecidae	*Angarosphex*	Rasnitsyn, 1977
Falsiformicidae	*Falsiformica*	Rasnitsyn, 1977
?SCOLIOIDEA-BETHYLOIDEA		
?Scolebythidae	*Cretabythus*	Evans, 1973
BETHYLOIDEA		
Bethylidae	*Archaepyris*	Evans, 1973
	Celonophamia	Evans, 1973
Cleptidae	*Procleptes*	Evans, 1969
	Hypocleptes	Evans, 1973
	Protamisega	Evans, 1973
Dryinidae	*Cretodryinus*	Rasnitsyn, 1977
POMPILOIDEA		
Pompilidae	*Pompilopterus*	Rasnitsyn, 1977
FORMICOIDEA		
Formicidae	*Sphecomyrma*	Wilson and Brown, 1967
	Cretomyrma	Rasnitsyn, 1977
	Paleomyrmex	Rasnitsyn, 1977
SPHECOIDEA		
Sphecidae	*Lisponema*	Evans, 1969
	Pittoecus	Evans, 1973
?SPHECOIDEA		
?Sphecidae	*Archisphex*	Evans, 1969
	Taimyrisphex	Evans, 1973
VESPOIDEA		
Masaridae	*Curiovespa*	Rasnitsyn, 1975

absence of Vespidae from Baltic Amber (Lower Oligocene) and other fossil resins, in which ants are abundant, is probably due to their relatively large size, which reduces the likelihood of their entrapment in the sticky tree resin. Spradbery (1973, p. 316), attributes their scarcity in sedimentary deposits to "the behavioral characteristics and paper nest structures which do not lend themselves to fossilization." As with any other fossil, the absence of an insect in the paleontological record provides no proof as to its actual occurrence in the past; one can only reconstruct and evaluate paleofaunas on the basis of those organisms that are represented. Therefore, it is conceivable that wasps were present earlier than the record indicates, but that conditions conducive to their preservation were lacking. The following does, however, provide information on the diversity of the group as we know it.

Cretaceous

The earliest record of the Vespoidea extends back to the Upper Cretaceous (Turonian). Two species of vespoid wasp have been found in a deposit of this age in the USSR — both assigned to the genus *Curiovespa* (Rasnitsyn, 1975). Unfortunately, nothing is known about the body structure of these insects but on the basis of their wing venation they are placed in the family Masaridae. The presence of two distinct species in the same deposit suggests that some diversification of the Vespoidea had taken place as early as the Upper Cretaceous, although nothing is known about the morphological character of these early wasps.

Paleocene

No Vespoidea from this period are known.

Eocene

The Eocene beds of Green River have yielded a surprisingly diverse assemblage of aculeates, but most of these belong to the Terebrantia or Sphecoidea; the only vespoid recovered from this deposit, *Didineis solidescens,* is of uncertain systematic position (Evans, 1966, p. 393). Scudder (1890) described this specimen as a sphecid of the subfamily Nyssoninae. However, Evans (1966) examined the type and concluded that it did not belong to the family Sphecidae, but was probably a eumenid, and tentatively assigned it to the genus *Alastor.*

Figure 2. Vespoid wasp from Eocene of British Columbia. Original photograph of specimen in Royal Ontario Museum, Toronto. Length of forewing, 12 mm.

Piton (1940), in a thesis on the Eocene fossil beds of Menat, France, described an assemblage of Vespoidea found in this sedimentary deposit. However, because the six specimens he described are all assigned to extant genera, and do not show the characters essential for such generic designation, Piton's taxonomic determinations are perforce questionable. Particularly dubious is his placement of one specimen in the family Vespidae, genus *Polistes*. Because the morphological features necessary for accurate taxonomic placement are obscured in this fossil, I prefer to place it in Vespoidea *incertae sedis*. The remaining five specimens are assigned to the Eumenidae *incertae sedis*.

Another vespoid species was recently recovered from a Middle Eocene deposit in British Columbia (M. V. H. Wilson, 1977). Although not formally described, the fossil clearly shows the characteristic venation of the vespoid complex (see Fig. 2), but could be either a vespid or a eumenid. Of course, one has no way of stating

with certainty that these early vespids were social. Within the Vespidae, divisions into subfamily and tribe are based primarily on behavioral rather than morphological characters. Furthermore, the morphological differences between the castes in any given species are often not obvious in the preserved fossils.

Oligocene

True vespids are first found in the Upper Oligocene shales of Florissant, Colorado and Rott, Germany, two highly productive fossiliferous deposits. These beds and other various localities listed in Table 3 have turned up an assemblage comprised of four genera and 14 species. It is quite remarkable that three of the four genera represented are extant and this supports the possibility that the Vespidae were essentially modern by the Oligocene. Furthermore, the diversification of taxa suggests a much earlier origin for the family than is evidenced by the fossil record.

Miocene

Scarcely any Vespidae are known from the Miocene, although this is most likely due to the overall dearth of deposits from this epoch. One vespid has been described from a deposit in Germany. This is *Polistes kirbyanus* and clearly belongs to the subfamily Polistinae. Other wasps from Miocene deposits have yet to be discovered, but one can assume that the wasp fauna of this age would be barely distinguishable from the wasp fauna of today.

FORMICOIDEA

The following review of the fossil history of the Formicidae provides important information on their dominance, distribution, and supposed habits during the Mesozoic and Cenozoic eras. In contrast to the Vespoidea, ants are the most abundant insects in Tertiary formations. This may be attributed to their foraging behavior on and around trees, which enhances their chances of preservation in amber. A rough total of 20,000 specimens representing some 200 species of ants has been studied (Table 4); this massive amount of work far exceeds the paleontological investigations carried out on any other family of insects. Several comprehensive monographs on the subject have been written, including *The Ants of the Baltic Amber* (Wheeler, 1914), and *The Fossil Ants of North America* (Carpenter, 1930), which are drawn on extensively in the following pages.

Cretaceous

The Cretaceous Period has, without question, provided more information on the early evolution of the ants than any other period, primarily because of the discovery in 1967 of two perfectly preserved worker ants in a New Jersey amber deposit. No doubt exists as to the primitive nature of these Cretaceous ants — both are members of the same species, *Sphecomyrma freyi* Wilson and Brown, and possess a mixture of wasp and ant characters. The petiole is distinctly ant-like, although the mandibles, which are short and bidentate, are very wasp-like (see Fig. 3A). A new subfamily, Sphecomyrminae, was named to accommodate *S. freyi* (Wilson, Carpenter, and Brown, 1967), and is considered ancestral to all known formicid subfamilies (see Taylor, 1978).

Since the discovery of *Sphecomyrma,* several other Cretaceous ants have been found, and these provide strong evidence that the family was widespread during this period. Dlussky (1975) described two new genera and three species, *Cretomyrma arnoldii, C. unicornis,* and *Paleomyrmex zherichini* (from a Late Cretaceous amber deposit in Yantardak, USSR) which he assigned to the Sphecomyrminae. It is of interest that the type of *P. zherichini* is the first winged male ant to be found in a Cretaceous deposit and provides the only indication of wing venation in the Sphecomyrminae (Fig. 3B). The figured specimen of *Cretomyrma unicornis* raises doubts as to its position in the Formicidae for it is a badly mangled, poorly preserved specimen and might be better assigned to Hymenoptera *incertae sedis.*[5] A fifth specimen, apparently a worker, has recently been discovered in the Cretaceous amber of Manitoba, Canada. Although not yet described, it undoubtedly belongs to the subfamily Sphecomyrminae (Wilson, personal communication).

Paleocene

No ants from the Paleocene are known, undoubtedly because so few fossiliferous beds containing insect remains from this epoch

[5]Dlussky (1975) also described several other "ants" which were found in Upper Cretaceous deposits in the Kzyl-Zhar of Russia. Three genera (3 species) were placed in the subfamily Ponerinae: *Petropone petiolata, Cretopone magna,* and *Archaeopone kzylzharica.* These are all fragmentary specimens, and, as figured by Dlussky, present no characters which would place them unequivocally in the Formicidae. They much more obviously belong in Hymenoptera *incertae sedis,* as does *Dolichomyrma longiceps* from the Upper Cretaceous of Kzyl-Zhar, which Dlussky put into Formicidae *incertae sedis.*

TABLE 3. VESPOIDEA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Masaridae		
**Curiovespa curiosa* Rasnitsyn	Kazakh, U.S.S.R.	Rasnitsyn, 1975
**Curiovespa magna* Rasnitsyn	Kazakh, U.S.S.R.	Rasnitsyn, 1975
EOCENE		
Eumenidae		
?*Alastor solidescens* (Scudder)	Green River, Wyoming	Evans, 1966
?*Rhygchium andrei* Piton	Menat, France	Piton, 1940
?*Odynerus manevali* Piton	Menat, France	Piton, 1940
?*Ancistrocerus eocenicus* Piton	Menat, France	Piton, 1940
?*Ancistrocerus berlandi* Piton	Menat, France	Piton, 1940
?*Eumenes projaponica* Piton	Menat, France	Piton, 1940
?Vespidae		
?*Polistes vergnei* Piton	Menat, France	Piton, 1940
OLIGOCENE		
Eumenidae		
Rhynchium sp. Theobald	Cereste, France	Theobald, 1937
Odynerus terryi Cockerell	Florissant, Colorado	Cockerell, 1909a
Odynerus wilmattae Cockerell	Florissant, Colorado	Cockerell, 1914
Odynerus oligopunctatus Theobald	Cereste, France	Theobald, 1937
?*Odynerus praesulptus* Cockerell	Florissant, Colorado	Cockerell, 1906
Odynerus percantusus Cockerell	Florissant, Colorado	Cockerell, 1914
?*Alastor rottensis* Statz	Rott, Germany	Statz, 1936
"Pseudonortania"† *sepulta* Timon-David	Camoins, France	Timon-David, 1944

Vespidae		
?**Paleovespa gillettei* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa florissantia* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa scudderi* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa relecta* Cockerell	Florissant, Colorado	Bequaert, 1930
**Paleovespa baltica* Cockerell	Baltic Amber	Cockerell, 1909b
**Paleovespa wilsoni* Cockerell	Florissant, Colorado	Cockerell, 1914
Polistes industrius Theobald	Cereste, France	Theobald, 1937
Polistes signata Statz	Rott, Germany	Statz, 1936
?*Polybia anglica* Cockerell	Isle of Wight, England	Cockerell, 1921a
Polybia oblita Cockerell	Isle of Wight, England	Cockerell, 1921b
Vespa bilineata Statz	Rott, Germany	Statz, 1936
Vespa cordifera Statz	Rott, Germany	Statz, 1936
Vespa nigra Statz	Rott, Germany	Statz, 1936
MIOCENE		
Vespidae		
Polistes kirbyanus Cockerell	Oeningen, Germany	Cockerell, 1914
?*Vespa attavina* Heer	Parschlug, Germany	Heer, 1849
?*Vespa crabroniformis* Heer	Radoboj, Croatia	Heer, 1867

?Of uncertain position within the Vespoidea — clearly Diploptera, but further determination impossible.
†*Pseudonortania* Timon-David is a junior homonym of *Pseudonortania* Soika, 1936.
*Extinct genera.

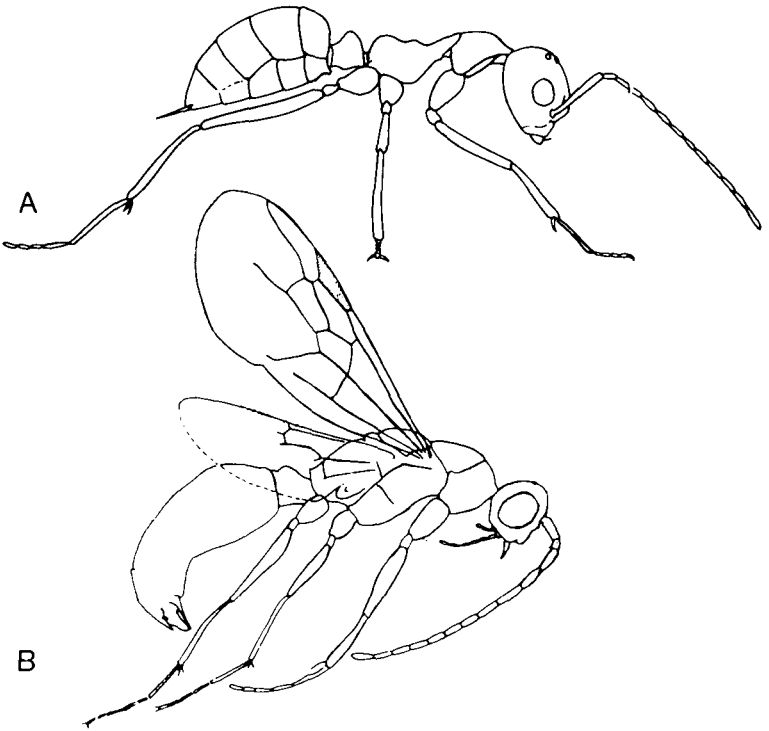

Figure 3A. *Sphecomyrma freyi* Wilson and Brown from the lower part of Upper Cretaceous of New Jersey. Drawing of holotype worker in Museum of Comparative Zoology, modified from Wilson, Carpenter, and Brown (1967). Length of body, 3.5 mm.

Figure 3B. *Paleomyrmex zherichini* Rasnitsyn from the lower part of the Upper Cretaceous of U.S.S.R. Drawing of holotype male in Paleontological Institute, Moscow, from Rasnitsyn, 1977. Length of body, 5.4 mm.

have been discovered. Mention is made by Brues (1936) of a piece of petrified wood containing what he considers ant borings, highly resemblant of borings made by *Camponotus* today. Although there is no clear-cut evidence that these borings represent *Camponotus* activity, or insect activity of any kind, it is conceivable that *Camponotus* was present in New Mexico during the Paleocene; several species have been dscribed from the Florissant Shales, Colorado (Upper Oligocene), and one from the Baltic Amber

(Lower Oligocene). In addition, it must be remembered that the Paleocene did not begin for at least 40 million years after the appearance of *Sphecomyrma freyi.*

Eocene

Very few fossil ants have been found in deposits of this age, and the determinations of many of these ant species are in doubt. Scudder (1877, 1878) described four supposed ants from the Green River formation, and five ants (1877) from the Quesnel Beds in British Columbia. Generic identifications on all of these fossils are to be considered dubious at best, and more likely incorrect (Carpenter, 1930).

In 1920, two species, *Oecophylla bartoniana* and *Formica heteroptera,* were described by Cockerell from an Eocene deposit in Bournemouth, England. Wheeler (1928) considered these ants formicines, but because the descriptions were based on wing fragments, he questioned their generic determinations. Similarly, Cockerell's *Formica eoptera* (1923a) from the Eocene of Texas is of uncertain position at both the generic and subfamily levels. *Archimyrmex rostratus* (Cockerell, 1923b) from the Eocene shales of Colorado is probably a myrmicine (Carpenter, 1930), and is the only Green River ant that can be placed with any certainty in a subfamily. Carpenter (1929) described *Eoponera berryi* from the Wilcox formation of Tennessee, and placed this ant in the subfamily Ponerinae. He suggests that it may be closely allied to the Neotropical genus *Dinoponera.* This is of interest because *Eoponera berryi* is the oldest known ant (Lower Eocene) to be assigned to a living subfamily of Formicidae.

Wilson (personal communication) mentions the recent discovery of three ants in a Middle Eocene amber deposit near Malvern, Arkansas, each belonging to a different subfamily. One belongs to the Dolichoderinae, genus *Iridomyrmex;* one is a formicine closely allied to the genus *Paratrechina,* and considered a relatively primitive, or "typical euformicine"; the last is a new genus of myrmicine, unique by virtue of its inflated postpetiole. These ants have yet to be formally described but they are nevertheless of paramount interest. The presence of these subfamilies in North America in the Eocene is strongly suggestive of their rapid evolution and dispersal during the Paleocene and perhaps during the Cretaceous.

Oligocene

The Baltic Amber is, most certainly, the best studied of all Tertiary insect deposits, and has revealed a great deal about the nature and diversity of Oligocene ants.[6] As of 1928, 11,711 ants (93 species) were examined from this deposit. Of this number, 1461 were studied by Mayr (1868); 690 by André (1895); and 9,560 by Wheeler (1914, 1928).

An examination of the ant fauna reveals wide representation at the subfamily and generic levels. All extant subfamilies of Formicidae are found in the amber with the exception of the Dorylinae and Leptanillinae. The absence of the Dorylinae is probably not due to selective exclusion on the part of the amber, but more likely indicates their absence from that part of the European continent during the Oligocene. Wheeler (1914) speculates that the foraging behavior of doryline ants should readily lead to entrapment in tree resin, but, in all probability, this group was then, as it is now, confined to the tropics. It is not surprising that the Leptanillinae are absent from the Baltic Amber; this is a small subfamily once considered a tribe of the Dorylinae, consisting of one genus and a few species; and although pantropical is hypogaeic and rarely encountered.

The Dolichoderinae and Formicinae together constitute 97 percent of all specimens and evidence indicates that these amber ants were already extraordinarily specialized. Workers of *Iridomyrmex goepperti* were found in a piece of amber (originally in the Königsberg collection) with several aphids. On the basis of this discovery, Wheeler (1914) concludes that Homoptera were attended by ants then much as they are today. The finding of several genera of paussid beetles (e.g., *Arthropterus, Cerapterites* and *Eopaussus*) in the Baltic Amber (Wasmann, 1929) suggests that myrmecophiles were established at this time. Perhaps most remarkable of all was the discovery of two *Lasius schiefferdeckeri* workers — each found with a mite attached to the base of the hind tibia, in precisely the

[6]Because the Baltic Amber was secondarily deposited in a clay bed of Lower Oligocene age, it is necessarily older than the glauconitic sand ("blue-earth" clay) in which it lies. How much older is uncertain. In some published accounts it is referred to as Eocene. However, since the composition of the Baltic Amber ant fauna is very similar to that of the Florissant Shales and other *bona fide* Oligocene deposits, I am following Zeuner (1939, p. 26) in referring to the amber as Lower Oligocene.

same position on each. This demonstrates almost certainly that by the Lower Oligocene mites had acquired distinct preferences for attachment on specific regions of their host's integument.

Almost as valuable as the Baltic Amber in providing a large and diverse assemblage of fossil ants is the Upper Oligocene deposit in Florissant, Colorado, studied by Carpenter (1930). The ant fauna of this deposit is strikingly similar to that of the Baltic Amber in many respects. It is interesting to note that roughly the same percentage of extant genera is found in both places; in the Florissant Shales this figure is given as 60 percent (Carpenter, 1930), in the Baltic Amber 56 percent (Wheeler, 1914). *Iridomyrmex* is clearly a dominant genus in the Baltic Amber, and although not so common in the Florissant Shales, a closely allied genus, *Protazteca,* comprises more than 25 percent of all specimens (Brown, 1973).

Another similarity between the two deposits is the relative percentages of the various subfamilies. As in the amber, the Dolichoderinae are predominant, comprising 60 percent of the total number of ants. The Formicinae comprise another 25 to 30 percent, and the Myrmicinae in each deposit are represented by five percent or less of the total specimens. This suggests that the ant fauna in the northern hemisphere was essentially homogenous during the Oligocene.

The remaining deposits of Oligocene age from which ants have been described are of relatively minor importance. Most of the specimens are fragmentary and the determinations dubious; nevertheless, a mention of them is certainly necessary. Specimens from Gurnet Bay, Isle of Wight, England, have been studied by Cockerell (1915) and Donisthorpe (1920). Cockerell described eight species of ants from this deposit but, because his generic determinations are based chiefly on highly variable measurements of wing fragments, they are of dubious significance. Donisthorpe examined a total of eight genera and fourteen species belonging to the subfamilies Ponerinae, Dolichoderinae, and Formicinae. Surprising is the large number of *Oecophylla* workers recovered (245); this genus is now restricted to Africa, India, and Australia, and is much more numerous in the Gurnet Bay deposit than in the Baltic Amber or Florissant Shales. This might be due to the difference in latitude between the deposits which would account for a warmer climate at Gurnet Bay later into the Tertiary than at the more northern deposits.

Another Lower Oligocene deposit which has provided beautifully preserved fossil ants is Aix-en-Provence, France. Several species have been described by Theobald (1937), who recognized four subfamilies: Myrmicinae (1 species); Ponerinae (1 species); Dolichoderinae (1 genus, 2 species); and Formicinae (3 genera, 9 species). Also described by Theobald (1937) is an Oligocene collection from Haut-Rhin, France, in which he recognizes the same four subfamilies (16 genera, 34 species). This fauna is very similar to that found in the Baltic Amber; in fact, Theobald has found five species which he considers identical to species in the Baltic Amber. In a deposit in Gard, France, Theobald (1937) describes two species, one a myrmicine, the other a dolichoderine.

Meunier (1917) has described four ant species from an Upper Oligocene deposit in Rott, Germany. These have been assigned to three genera: *Formica, Ponera,* and *Myrmica.* The specimens are well-preserved, as may be seen in Meunier's photographs, but his generic determinations are questionable.

In 1957, two female reproductives of the same species were discovered in an Upper Oligocene deposit in Argentina. The authors described the species as *Ameghinoia piatnitskyi* and placed it in the subfamily Ponerinae (Viana and Haedo-Rossi, 1957). E. O. Wilson (personal communication) is highly sceptical of the placement of *A. piatnitskyi* in the Ponerinae, and thinks that it is very clearly a myrmeciine. This is quite extraordinary because no other fossil ants have been recovered from South America, and more importantly, if Wilson is correct, this is the first indication that the Myrmiciinae were so widespread by the Oligocene.

Miocene

The deposits of Miocene age which have provided the greatest number of ant specimens have been the Oeningen beds in Germany, and the Radoboj formation in Croatia. Approximately 60 species of ants from these places were described by the Swiss myrmecologist Heer (1849, 1856, 1867), but his generic assignments are necessarily questionable in terms of present-day concepts of a formicid genus. Regrettably, the type specimens which are essential to a revision of this fossil fauna are believed to be lost.

A few species were described by Emery (1891) in Sicilian amber, presumed to be Miocene, but these, like the specimens studied by Heer, are of questionable generic position.[7]

Another Miocene amber deposit has been found in Chiapas, Mexico, from which some one hundred ants have been recovered. Unfortunately, the majority of these are fragmentary, or otherwise too poor for determination. The assemblage does, however, suggest that the ant fauna in Mexico during the Miocene was essentially the same as might be found in that region today (Brown, 1973).

Fujiyama (1970) described a single ant from the Chōjabaru formation in Japan (middle Miocene) which he named *Aphaenogaster axila,* thought to be closely allied to the subgenus *Deromyrma.* This is not particularly unusual inasmuch as *Aphaenogaster* is a world-wide genus, and several species are found in Japan today.

Perhaps the most interesting of all Miocene material is an ant colony of *Oecophylla leakeyi* found in Kenya (Wilson and Taylor, 1964). This is the first record of an actual, although fragmented, ant colony and contains a total of 366 specimens: 197 larvae, 105 worker pupae, and at least 64 workers. No Nearctic fossils of *Oecophylla* are known, but the species is well represented in European Tertiary deposits. Wilson and Taylor suggest on the basis of these fossil specimens that *Oecophylla* is a morphologically stable paleotropical genus which has persisted through most of the Tertiary with very little specialization.

APOIDEA

The Apoidea form an interesting complex of social insects. Unlike the other social insect groups that are consistent in their degree of social achievement at the ordinal level (Isoptera), family level (Formicidae), and virtually the subfamily level (Vespinae), the Apoidea present a wide spectrum of social behavior at the generic level. Evidence suggests that eusociality has arisen in the bees at least eight times (Michener, 1962; Wilson, 1971), which may explain this variance. Nevertheless, it is noteworthy that of roughly 20,000 existing species of bees only a small minority are thought to be presocial and eusocial (Wilson, 1971). Why sociality in the Apoidea

[7]These generic determinations are currently being reviewed by Dr. W. L. Brown, Jr.

TABLE 4. FORMICOIDEA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Sphecomyrminae		
**Sphecomyrma freyi* Wilson and Brown	New Jersey, U.S.A.	Wilson, Carpenter and Brown, 1967
?**Sphecomyrma* sp.	Manitoba, Canada	Wilson, pers. comm.
**Cretomyrma arnoldii* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
**Cretomyrma unicornis* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
**Paleomyrmex zherichini* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
EOCENE		
Myrmicinae		
**Archimyrmex rostratus* Cockerell	Florissant, Colorado	Carpenter, 1930
Formicinae		
Oecophylla bartoniana Cockerell	Bournemouth, England	Cockerell, 1920
Formica eoptera Cockerell	Texas, U.S.A.	Carpenter, 1930
Formica heteroptera Cockerell	Bournemouth, England	Cockerell, 1920
?*Paratrechina* sp.	Arkansas, U.S.A.	Wilson, pers. comm.
Ponerinae		
**Eoponera berryi* Carpenter	Tennessee, U.S.A.	Carpenter, 1929
Dolichoderinae		
Iridomyrmex sp.	Arkansas, U.S.A.	Wilson, pers. comm.
OLIGOCENE		
Myrmiciinae		
**Ameghinoia piatnitskyi* Viana and Haedo-Rossi	Argentina	Viana and Haedo-Rossi, 1957
Ponerinae		
Brachyponera dubia Theobald	Haut-Rhin, Germany	Theobald, 1937a

**Archiponera wheeleri* Carpenter	Florissant, Colorado	Carpenter, 1930
**Prionomyrmex longiceps* Mayr	Baltic Amber	Wheeler, 1914
**Procerapachys annosus* Wheeler	Baltic Amber	Wheeler, 1914
**Procerapachys favosus* Wheeler	Baltic Amber	Wheeler, 1914
**Bradoponera meieri* Mayr	Baltic Amber	Wheeler, 1914
Ectatomma europaeum Mayr	Baltic Amber	Wheeler, 1914
**Electoponera dubia* Wheeler	Baltic Amber	Wheeler, 1914
Platythyrea primaeva Wheeler	Baltic Amber	Wheeler, 1914
Euponera calcarea Theobald	Haut-Rhin, Germany	Theobald, 1937
Euponera succinea (Mayr)	Baltic Amber	Wheeler, 1914
Euponera crawleyi Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Euponera globiventris Theobald	Haut-Rhin, Germany	Theobald, 1937
Ponera atavia Mayr	Baltic Amber	Wheeler, 1914
Ponera minuta Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Ponera elegantissima Meunier	Rott, Germany	Meunier, 1923
Ponera hypolitha Cockerell	Isle of Wight, England	Cockerell, 1915
Ponera rhenana Meunier	Rott, Germany	Meunier, 1917
?*Ponera gracilicornis* Mayr	Baltic Amber	Wheeler, 1914
**Emplastus emeryi* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
**Syntaphus wheeleri* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Pseudomyrmicinae		
Pseudomyrma extincta Carpenter	Florissant, Colorado	Carpenter, 1930
Myrmicinae		
Aphaenogaster mayri Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster donisthorpei Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster maculipes Theobald	Haut-Rhin, Germany	Theobald, 1937
Aphaenogaster maculata Theobald	Aix-en-Provence, France	Theobald, 1937
Aphaenogaster sommerfeldti Mayr	Baltic Amber	Wheeler, 1914
Aphaenogaster oligocenica Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Myrmicinae (continued)		
Aphaenogaster mersa Wheeler	Baltic Amber	Wheeler, 1914
Sima klebsi Wheeler	Baltic Amber	Wheeler, 1914
Sima ocellata Mayr	Baltic Amber	Wheeler, 1914
Sima simplex Mayr	Baltic Amber	Wheeler, 1914
Sima angustata Mayr	Baltic Amber	Wheeler, 1914
Sima lacrimarum Mayr	Baltic Amber	Wheeler, 1914
Sima klebsi Theobald	Haut-Rhin, Germany	Theobald, 1937
Sima oligocenica Theobald	Gard, France	Theobald, 1937
Monomorium pilipes Mayr	Baltic Amber	Wheeler, 1914
Monomorium mayrianum Wheeler	Baltic Amber	Wheeler, 1914
Erebomyrma antiqua (Mayr)	Baltic Amber	Wheeler, 1914
Erebomyrma thorali Theobald	Haut-Rhin, Germany	Theobald, 1937
Vollenhovia beyrichi (Mayr)	Baltic Amber	Wheeler, 1914
Vollenhovia prisca (Andre)	Baltic Amber	Wheeler, 1914
Stenamma berendti (Mayr)	Baltic Amber	Wheeler, 1914
**Electromyrmex klebsi* Wheeler	Baltic Amber	Wheeler, 1914
**Agroecomyrmex duisburgi* (Mayr)	Baltic Amber	Wheeler, 1914
Myrmica longispinosa Mayr	Baltic Amber	Wheeler, 1914
Myrmica archaica Meunier	Rott, Germany	Meunier, 1915
**Nothomyrmica rudis* (Mayr)	Baltic Amber	Wheeler, 1914
**Nothomyrmica intermedia* Wheeler	Baltic Amber	Wheeler, 1914
**Nothomyrmica rugosostriata* (Mayr)	Baltic Amber	Wheeler, 1914
**Nothomyrmica petiolata* (Mayr)	Baltic Amber	Wheeler, 1914
Leptothorax gracilis Mayr	Baltic Amber	Wheeler, 1914

Leptothorax glaesarius Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax longaevus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax hystriculus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax placivus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax gurnetensis Cockerell	Isle of Wight, England	Cockerell, 1915
Leucotaphus cockerelli Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
**Stiphromyrmex robustus* (Mayr)	Baltic Amber	Wheeler, 1914
**Parameranoplus primaevus* Wheeler	Baltic Amber	Wheeler, 1914
Stigmomyrmex venustus Mayr	Baltic Amber	Wheeler, 1914
**Enneamerus reticulatus* Mayr	Baltic Amber	Wheeler, 1914
Solenopsis maxima (Förster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis valida (Förster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis major Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis superba Förster	Haut-Rhin, Germany	Theobald, 1937
Solenopsis försteri Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis blanda Theobald	Haut-Rhin, Germany	Theobald, 1937
Pheidole tertiaria Carpenter	Florissant, Colorado	Carpenter, 1930
Messor sculpteratus Carpenter	Florissant, Colorado	Carpenter, 1930
Pogonomyrmex fossilis Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex rugosus Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
**Cephalomyrmex rotundatus* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderinae		
**Protaneuretus succineus* Wheeler	Baltic Amber	Wheeler, 1914
**Paraneuretus tornquisti* Wheeler	Baltic Amber	Wheeler, 1914
**Paraneuretus longipennis* Wheeler	Baltic Amber	Wheeler, 1914
**Mianeuretus mirabilis* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus oviformis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus coquandi Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Dolichoderinae (continued)		
Dolichoderus bruneti Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus explicans Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus affectus Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus balticus Theobald	Aix-en-Provence, France	Theobald, 1937
Dolichoderus balticus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus oviformis Theobald	Gard, France	Theobald, 1937
Dolichoderus antiquus Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus rohweri Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus cornutus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus passalomma Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus elegans Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus mesosternalis Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus vexillarius Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus sculpteratus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus tertiarius (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus longipennis Mayr	Baltic Amber	Wheeler, 1914
Dolichoderus britannicus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus gurnetensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Dolichoderus ovigerus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus vectensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Iridomyrmex goepperti Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex goepperti Mayr	Baltic Amber	Wheeler, 1914
Iridomyrmex geinitzi Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex geinitzi (Mayr)	Baltic Amber	Wheeler, 1914

Iridomyrmex breviantennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex florissantius Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex obscurans Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex constrictus (Mayr)	Baltic Amber	Wheeler, 1914
Iridomyrmex samlandicus Wheeler	Baltic Amber	Wheeler, 1914
Iridomyrmex oblongiceps Wheeler	Baltic Amber	Wheeler, 1914
Protazteca elongata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca quadrata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca capitata Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum miocenicum Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum oligocenicum Wheeler	Baltic Amber	Wheeler, 1914
Liometopum scudderi Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex gracilis Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex coloradensis Carpenter	Florissant, Colorado	Carpenter, 1930
Asymphylomyrmex balticus Wheeler	Baltic Amber	Wheeler, 1914
Pityomyrmex tornquisti Wheeler	Baltic Amber	Wheeler, 1914
Miomyrmex impactus (Cockerell)	Florissant, Colorado	Carpenter, 1930
Miomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
Petraeomyrmex minimus Carpenter	Florissant, Colorado	Carpenter, 1930
Formicinae		
Plagiolepis succini André	Baltic Amber	Wheeler, 1914
Plagiolepis klinsmanni Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis kuenowi Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis squamifera Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis singularis Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis solitaria Mayr	Baltic Amber	Wheeler, 1914
**Rhopalomyrmex pygmaeus* Mayr	Baltic Amber	Wheeler, 1914
Dimorphomyrmex theryi Emery	Baltic Amber	Wheeler, 1914, 1929
Dimorphomyrmex mayri Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Formicinae (continued)		
Gesomyrmex annectens Wheeler	Baltic Amber	Wheeler, 1914
Gesomyrmex expectans Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex miegi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Mayr	Baltic Amber	Wheeler, 1929
**Prodimorphomyrmex primigenius* Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla superba Theobald	Haut-Rhin, Germany	Theobald, 1937
Oecophylla brischkei Mayr	Baltic Amber	Wheeler, 1914
Oecophylla brevinodis Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla megarche Cockerell	Isle of Wight, England	Donisthorpe, 1920
Oecophylla atavina Cockerell	Isle of Wight, England	Cockerell, 1915
Oecophylla perdita Cockerell	Isle of Wight, England	Cockerell, 1915
Prenolepis henschei Mayr	Baltic Amber	Wheeler, 1914
Prenolepis pygmaea Mayr	Baltic Amber	Wheeler, 1914
Lasius schiefferdeckeri Mayr	Baltic Amber	Wheeler, 1914
Lasius pumilus Mayr	Baltic Amber	Wheeler, 1914
Lasius epicentrus Theobald	Aix-en-Provence, France	Theobald, 1937
Lasius chambonensis Piton and Theobald	Lac Chambon, France	Piton and Theobald, 1935
Lasius tertiarius Zalessky	Ukraine, U.S.S.R.	Zalessky, 1949
Lasius punctulatus Mayr	Baltic Amber	Wheeler, 1914
Lasius nemorivagus Wheeler	Baltic Amber	Wheeler, 1914
Lasius edentatus Mayr	Baltic Amber	Wheeler, 1914
Tetramorium peritulus (Cockerell)	Florissant, Colorado	Wilson, 1955
Eoformica eocenica Cockerell	Florissant, Colorado	Cockerell, 1921c

Formica flori Mayr	Baltic Amber	Wheeler, 1914
Formica flori Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica horrida Wheeler	Baltic Amber	Wheeler, 1914
Formica phaethusa Wheeler	Baltic Amber	Wheeler, 1914
Formica clymene Wheeler	Baltic Amber	Wheeler, 1914
Formica constricta (Mayr)	Baltic Amber	Wheeler, 1914
Formica strangulata Wheeler	Baltic Amber	Wheeler, 1914
Formica tripartita Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica alsatica Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica serresi Theobald	Aix-en-Provence, France	Theobald, 1937
Formica latinodosa Theobald	Aix-en-Provence, France	Theobald, 1937
Formica oculata Theobald	Aix-en-Provence, France	Theobald, 1937
Formica minutula Theobald	Aix-en-Provence, France	Theobald, 1937
Formica sepulta Theobald	Aix-en-Provence, France	Theobald, 1937
Formica robusta Carpenter	Florissant, Colorado	Carpenter, 1930
Formica cockerelli Carpenter	Florissant, Colorado	Carpenter, 1930
Formica grandis Carpenter	Florissant, Colorado	Carpenter, 1930
Formica masculipennis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Formica pitoni Theobald	Lac Chambon, France	Piton and Theobald, 1935
Formica bauckhorni Meunier	Rott, Germany	Meunier, 1917
Formica auxillacensis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Glaphyomyrmex oligocenicus Wheeler	Baltic Amber	Wheeler, 1914
Pseudolasius boreus Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dryomyrmex claripennis Wheeler	Baltic Amber	Wheeler, 1914
Glaphyromyrmex oligocenicus Theobald	Haut-Rhin, Germany	Theobald, 1937
Camponotus mengei Mayr	Baltic Amber	Wheeler, 1914
Camponotus mengei Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4. (CONCLUDED)

Geological Age	Locality	References
OLIGOCENE Formicinae (continued)		
Camponotus vehemens Förster	Haut-Rhin, Germany	Theobald, 1937
Camponotus longiventris Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus saussurei Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus penninervis Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus fuscipennis Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus microcephalus Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus petrifactus Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus brodiei Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
MIOCENE		
Ponerinae		
Ponera umbra Popov	Caucasus, U.S.S.R.	Popov, 1933
Myrmicinae		
Aphaenogaster axila Fujiyama	Chôjabaru, Japan	Fujiyama, 1970
Formicinae		
Camponotus obesus Piton	Joursac, France	Piton and Theobald, 1935
Camponotus tokunagai Naora	China	Naora, 1933
**Pseudocamponotus elkoanus* Carpenter	Elko, Nevada	Carpenter, 1930
Solenopsis longaevus Heer	Radoboj, Croatia	Poncracz, 1928
Formica cantalica Piton	Joursac, France	Piton and Theobald, 1935
Lasius crispus Piton	Joursac, France	Piton and Theobald, 1935
Lasius martynovi Popov	Caucasus, U.S.S.R.	Popov, 1933
Oecophylla leakeyi Wilson and Taylor	Kenya	Wilson and Taylor, 1964

*Extinct genera.

is so highly polyphyletic remains unanswered, and is a problem unlikely to be resolved by the geological past.

However, the fossil record does provide intriguing information on the evolution of the bees and indicates that their sociality may well have been established prior to the Oligocene. The following survey of the fossil Apoidea is indicative of the diversity of bees which have been found (Table 5). Those species which were described by early 19th century entomologists (Latreille, Heer, Heyden, etc.) are excluded from this coverage because these were uniformly assigned to modern genera.[8] Cockerell (1909) claims that most of these species actually belonged to quite different and extinct genera.

Oligocene

The earliest bees in the fossil record are found in the Baltic Amber, of Lower Oligocene age. The bees in this deposit are well-diversified (Zeuner and Manning, 1976), and the most prevalent apoid genus in the amber, *Electrapis,* is thought to have been social. Cockerell (1909) based this conclusion on the occurrence of many specimens of *Electrapis meliponoides* crowded together in a small piece of amber, a suggestive but certainly not conclusive deduction. Zeuner (1944, 1951), however, believed *Electrapis* to be social based on its pollen collecting apparatus. The extent to which social behavior was developed in this genus nevertheless remains a matter of conjecture. *Electrapis* is considered by some to be directly ancestral to the highly eusocial *Apis,* although Kelner-Pillault (1974) disagrees with this relationship. She suggests that *Electrapis* is actually a long extinct genus which possessed many primitive characters and represents an evolutionary side-line of the Apoidea. Both hypotheses are highly conjectural.

The presence of long-tongued bees such as *Electrapis* suggests that the Baltic Amber bees were rather specialized. Tongue structure is assumed to have evolved in response to various morphological changes (i.e., longer corollas) which took place during the evolution of the angiosperms (Michener, 1974). Short-tongued bees such as the colletids are considered the more primitive members of the Apoidea and are representative of bee radiation that occurred at a time when most of the angiosperms had shallow flowers (Michener, 1974).

---

[8]For a listing of these specimens, see Zeuner and Manning (1976).

In Late Oligocene deposits, the Apoidea are extremely well represented. Six major families of bees are known from this epoch: Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae, and Apidae. A total of 29 genera are represented, many of which are extant. Several specimens belonging to *Chalcobombus* and *Bombus* are described from deposits in both Europe and North America suggesting widespread radiation of this specialized group of bees by the Early Oligocene. In the Late Oligocene, bees very similar to *Apis mellifera* are found. Manning (1952) feels that some species from the Rott Shales possess almost all the necessary characters for placement in the genus *Apis* (Fig. 4). Moreover, in the Dominican Amber of Oligocene-Miocene age, several *Trigona* workers are found, providing convincing proof that social behavior was well established at this time (Michener, 1974).

Figure 4. *Apis henshawi* Cockerell from Upper Oligocene of Rott, Germany. Original photograph of holotype in Museum of Comparative Zoology. Length of body, 15 mm.

Miocene

By the Miocene, the bee fauna is essentially modern. In Chiapas Amber from Mexico, bees have been discovered that are so similar to an existing Neotropical species that they have been assigned to the same subgenus, *Trigona* (*Nogueirapis*), and are scarcely different at the specific level (Wille, 1959). Fujiyama (1970) mentions the discovery of a fossil bee in a Japanese Miocene deposit and states that, "There is no room for doubt that this is a species of honeybee."

A review of the fossil record reveals the following about the evolution of the bees. 1) We know that the Early Oligocene fauna is a mixture of primitive and advanced genera, although it appears to be dominated by fairly advanced species. By the end of this epoch, the fauna is modern in overall character. 2) We know that sociality had clearly arisen by the end of the Oligocene, and possibly much earlier. And 3) by the Miocene, the bees were virtually indistinguishable from the bees of today. Six families of bees are represented in the Oligocene: including the phylogenetically advanced Apidae with six genera and 22 species. Such diversity of relatively advanced bees is indicative of either a much longer history of the group than is evidenced by the fossil record, or a fairly short history characterized by the rapid speciation and explosive radiation of the group.

The bees are clearly derived from the spheciform wasps, although nothing is known about the nature of this sphecid ancestor (Wilson, 1971; Michener, 1974). In 1964, just prior to his death, F. J. Manning was investigating a sphecid from the Jurassic beds of Lerida Province, Spain, which "he thought might be (or be closely related to) the ancestor of the bees" (Zeuner and Manning, 1976, p. 155). This would be an astounding find if true, and it is unfortunate that nothing more is known — either about the specimen or about Manning's reasons for thinking it ancestral to the bees.

The distinction between the Sphecoidea and the Apoidea is sufficiently subtle as to make determinations of fossil compressions extremely difficult. The presence of plumose hairs and enlarged basitarsi, characters which are important apoid features, rarely survive preservation unless the insect is preserved in amber.

The origin of the bees remains a subject of much speculation. It is believed that "insect-plant interactions played a key role in the origin of the angiosperm flower and component structures" (Hickey

and Doyle, 1977, p. 92). Conversely, angiosperms have been instrumental to the evolutionary success of the Apoidea. On the basis of the evolutionary dependence of the two groups, can anything be said about their relationship in geological time? Two possibilities present themselves: 1) the angiosperms evolved first and were initially wind pollinated[9] or pollinated by arthropods other than Hymenoptera (e.g., Coleoptera, Diptera, Thysanoptera, possibly spiders); and 2) the first bees evolved from sphecid wasps prior to the origin of the angiosperms by adapting themselves to feeding on pteridosperm pollen or reproductive organs.

A closer look at these possibilities is warranted. Coleoptera and Diptera are found in the fossil record at least by the Triassic. This supports the argument that they could have served as vectors for dispersal of angiosperm pollen. The question arises, if these insects were capable of performing essential roles as pollinators, why didn't angiosperms arise earlier in the Mesozoic than the Cretaceous? Regal (1977) suggests that the limiting factor to angiosperm dispersal was the presence of seed-carrying birds and mammals. He argues that this method of seed dispersal, acting in conjunction with insect pollination, provided the selective advantages behind the subsequent primary radiation of the angiosperms. This is a sound argument, but says little about the insects which may have been pollinating these early plants. It would seem that successful dispersal of flowering plants is dependent on efficiency at two levels — pollination and seed dispersal. The explosive radiation of the angiosperms during the Cretaceous indicates that the more specialized insect pollinators, the bees, may have been present in order to explain this success.

This might support the possibility that pollen collecting bees had already evolved by the time the first angiosperms appeared. According to Wilson (1971, p. 75), the "Apoidea can be loosely characterized as sphecoid wasps that have specialized in collecting pollen instead of insect prey as larval food." The possibility, however speculative, exists that bees evolved in response to the food source presented by the pteridosperms but subsequently abandoned this resource when the angiosperms appeared. Certainly one way of accounting for the explosive radiation of the angiosperms would be

[9]Stebbins (1970, p. 323) suggests that the earliest angiosperms were not wind pollinated.

TABLE 5. APOIDEA IN THE FOSSIL RECORD.[10]

Geological Age	Locality
EOCENE	
?Apidae	
Probombus hirsutus Piton	Menat, France
OLIGOCENE	
Halictidae	
**Cyrtapis anomalis* Cockerell	Florissant, Colorado
Halictus ruissatelensis Timon-David	Marseille, France
Halictus florissantellus Cockerell	Florissant, Colorado
Halictus miocenicus Cockerell	Florissant, Colorado
Halictus scudderiellus Cockerell	Florissant, Colorado
Andrenidae	
Andrena wrisleyi Salt	Baltic Amber
Andrena clavula Cockerell	Florissant, Colorado
Andrena grandipes Cockerell	Florissant, Colorado
Andrena hypolitha Cockerell	Florissant, Colorado
Andrena lagopus Latreille	Florissant, Colorado
Andrena percontusa Cockerell	Florissant, Colorado
Andrena sepulta Cockerell	Florissant, Colorado
**Lithandrena saxorum* Cockerell	Florissant, Colorado
**Pelandrena reducta* Cockerell	Florissant, Colorado
**Libellulapis antiquorum* Cockrell	Florissant, Colorado
**Libellulapis wilmattae* Cockerell	Florissant, Colorado
Melittidae	
**Ctenoplectrella dentata* Salt	Baltic Amber
**Ctenoplectrella viridiceps* Cockerell	Baltic Amber
**Ctenoplectrella splendens* Kelner-Pillault	Baltic Amber
**Glyptapis fuscula* Cockerell	Baltic Amber
**Glyptapis mirabilis* Cockerell	Baltic Amber
**Glyptapis neglecta* Salt	Baltic Amber
**Glyptapis reducta* Cockerell	Baltic Amber
**Glyptapis reticulata* Cockerell	Baltic Amber
Melitta willardi Cockerell	Baltic Amber
Megachilidae	
Anthidium mortuum (Meunier)	Rott, Germany
Anthidium exhumatum Cockerell	Florissant, Colorado
Anthidium scudderi Cockerell	Florissant, Colorado
**Dianthidium tertiarium* Cockerell	Florissant, Colorado
**Lithanthidium pertriste* Cockerell	Florissant, Colorado
Heriades bowditchi Cockerell	Florissant, Colorado
Heriades halictinus Cockerell	Florissant, Colorado
Heriades laminarum Cockerell	Florissant, Colorado
Heriades mersatus Cockerell	Florissant, Colorado

[10]See Zeuner and Manning (1976) for reference citations.

TABLE 5. (CONTINUED)

Geological Age	Locality
OLIGOCENE Megachilidae (continued)	
Heriades mildredae Cockerell	Florissant, Colorado
Heriades priscus Cockerell	Florissant, Colorado
Heriades saxosus Cockerell	Florissant, Colorado
Megachile praedicta Cockerell	Florissant, Colorado
Osmia carbonum Heyden	Rott, Germany
Anthophoridae	
Ceratina disrupta Cockerell	Florissant, Colorado
Xylocopa friesei Statz	Rott, Germany
Tetralonia berlandi Theobald	Gard, France
Anthophora melfordi Cockerell	Florissant, Colorado
**Anthophorites gaudryi* Oustalet	Corent, France
**Protomelecta brevipennis* Cockerell	Florissant, Colorado
Apidae	
**Chalcobombus hirsutus* Cockerell	Baltic Amber
**Chalcobombus humilis* Cockerell	Baltic Amber
**Chalcobombus martialis* Cockerell	Baltic Amber
Bombus florissantensis (Cockerell)	Florissant, Colorado
**Sophrobombus fatalis* Cockerell	Baltic Amber
Trigona dominicana Wille and Chandler	Dominican Amber
Trigona eocenica Kelner-Pillault	Baltic Amber
**Electrapis apoides* Manning	Baltic Amber
**Electrapis meliponoides* (Buttel-Reepen)	Baltic Amber
**Electrapis indecisus* (Cockerell)	Baltic Amber
**Electrapis tristellus* (Cockerell)	Baltic Amber
**Electrapis palmnickenensis* (Roussy)	Baltic Amber
**Electrapis minuta* Kelner-Pillault	Baltic Amber
**Electrapis bombusoides*	Baltic Amber
Electrapis proava (Menge)	Baltic Amber
Electrapis tornquisti Cockerell	Baltic Amber
Apis cuenoti Theobald	Cereste, France
Apis henshawi Cockerell	Rott, Germany
Apis henshawi dormitans (Cockerell)	Rott, Germany
Apis henshawi kaschkei (Statz)	Rott, Germany
Apis aquitanensis de Rilly	Aix-en-Provence, France

TABLE 5. (CONCLUDED)

Geological Age	Locality
MIOCENE	
Halictidae	
Halictus schemppi (Armbruster)	Randeck, Germany
Andrenidae	
Andrena primaeva Cockerell	Oeningen, Germany
Megachilidae	
Lithurge adamitica (Heer)	Oeningen, Germany
Megachile amaguensis Cockerell	Siberia, U.S.S.R.
Osmia antiqua Heer	Oeningen, Germany
Osmia nigra Zeuner and Manning	Oeningen, Germany
Anthophoridae	
Xylocarpa jurinei (Heer)	Oeningen, Germany
Xylocopa hydrobiae Zeuner	Biebrich, Germany
Xylocopa senilis Heer	Oeningen, Germany
**Anthophorites thoracica* Heer	Radoboj, Croatia
**Anthophorites longaeva* Heer	Radoboj, Croatia
**Anthophorites mellona* Heer	Oeningen, Germany
**Anthophorites titania* Heer	Oeningen, Germany
**Anthophorites tonsa* Heer	Oeningen, Germany
**Anthophorites veterana* Heer	Oeningen, Germany
Apidae	
Bombus abavus Heer	Oeningen, Germany
Bombus proavus Cockerell	Latah, Washington
Trigona succini (Tosi)	Sicilian Amber
Trigona sicula (Tosi)	Sicilian Amber
Trigona silacea Wille	Chiapas, Mexico
Trigona devicta Kerr and Maule	Burma Amber
Apis armbrusteri armbrusteri Zeuner	Württemburg, Germany
Apis armbrusteri scharmanni (Armbruster)	Württemburg, Germany
Apis armbrusteri scheeri (Armbruster)	Württemburg, Germany
Apis armbrusteri scheuthlei (Armbruster)	Württemburg, Germany
Apis catanensis avolii Roussi	Sicilian Amber
Apis melisuga (Handlirsch)	Italy

*Extinct genera.

the explanation that the insect pollinators so important to their success were pre-adapted as pollination vectors. It is interesting to note at this point that bees have been observed foraging on conifer pollen in areas where other food resources are scarce. Ray Angelo (personal communication, May, 1978) reports observing *Colletes* sp. foraging in high numbers on *Juniperus virginiana* pollen cones. This is noteworthy in two respects: 1) this conifer is the only readily available pollen source in the particular habitat where observations took place (Concord, Mass.), and 2) the bees foraging on the tree are members of the primitive bee family Colletidae. This suggests that they are generalized enough to have retained the ability to forage on gymnosperm pollen. Nevertheless, the hypothesis that bees evolved before the advent of the angiosperms is highly speculative, and remains a difficult theory to prove. The possibility of a pre-angiosperm origin for the bees implies that the Apoidea, and possibly sociality in the Apoidea, may be older than indicated by the fossil record. An inherent problem, of course, is whether or not these early bees would be recognizable as such, or would be mistaken for sphecid wasps. The discovery of additional Cretaceous amber might well provide valuable insight into this problem.

SUMMARY

Wheeler writes in his 1928 book, "from the lowest to the highest forms in the series, all animals are at some time in their lives immersed in some society." It is the elaboration or evolution of these habits that leads to the eusocial behavior found in the Isoptera and certain groups of the Hymenoptera. The preceding account has examined insect sociality from a paleontological perspective in the hope that it will provide insight into the antiquity of this behavioral phenomenon. In addition, it has provided information on certain aspects of the evolution of the four major groups of social insects.

The Isoptera are highly eusocial at the ordinal level and evidence suggests an ancient origin for the group. The oldest fossil termite known is from a Late Cretaceous deposit in Canada. The presence of a distinct humeral suture at the wing base indicates that social behavior was developed in the Isoptera at this time. It is furthermore presumed that the termites arose in the early Mesozoic or possibly earlier, and from "protoblattoid" or blattoid stock. The hypogaeic lifestyle of most termites is not conducive to their

preservation as fossils and this may explain their absence in pre-Cretaceous deposits.

The first Hymenoptera appear in the Triassic and belong to the primitive family Xyelidae (Symphyta). Social Hymenoptera are not, however, found in the fossil record until the Upper Cretaceous. The ant species discovered in deposits of this age are more primitive than any now existing and have been of paramount importance in our understanding of ant phylogeny. By the mid-Tertiary, the ant fauna was extremely diverse; by the Miocene, the genera were essentially modern, and geographic distribution of the ants was apparently similar to that of today.

The Vespoidea although not very numerous in fossil deposits, have been found as far back as the Late Cretaceous, represented by one specimen assignable to the Masaridae. The presence of several vespoids in Eocene deposits strongly supports the possibility that social wasps evolved during the Late Cretaceous or Early Paleocene.

Apoidea extend into the fossil record only as far as the Oligocene, although it is speculated that they may have evolved much earlier. This is suggested by the fact that the bee fauna was essentially modern by the end of the Oligocene and also because the interdependence of angiosperms and bees suggests a co-evolutionary relationship beginning sometime in the Cretaceous.

Any discussion of sociality in the geological past must necessarily involve a certain amount of speculation. Morphological characters play an essential role in the analysis of an insect's social status, an example of this being the presence of the humeral suture in *Cretatermes*. In those social insect groups possessing very little morphological variation between castes, recognition of such social distinctions in the fossils is virtually impossible. It is generally assumed that extinct species belonging to extant genera possessed a similar type of social behavior in the past as is exhibited by the group today. To speculate further about the social habits of fossil insects is simply not possible. The mechanisms behind the evolution of eusociality in the insects remain unknown, yet the success of this form of social behavior is unquestioned. Only the recovery of additional material will provide evidence to further elucidate our understanding of the paleontological record of these insects.

As the record now stands, it is possible to state with a fair degree of certainty that insect sociality had evolved by the middle of the Cretaceous and perhaps much earlier.

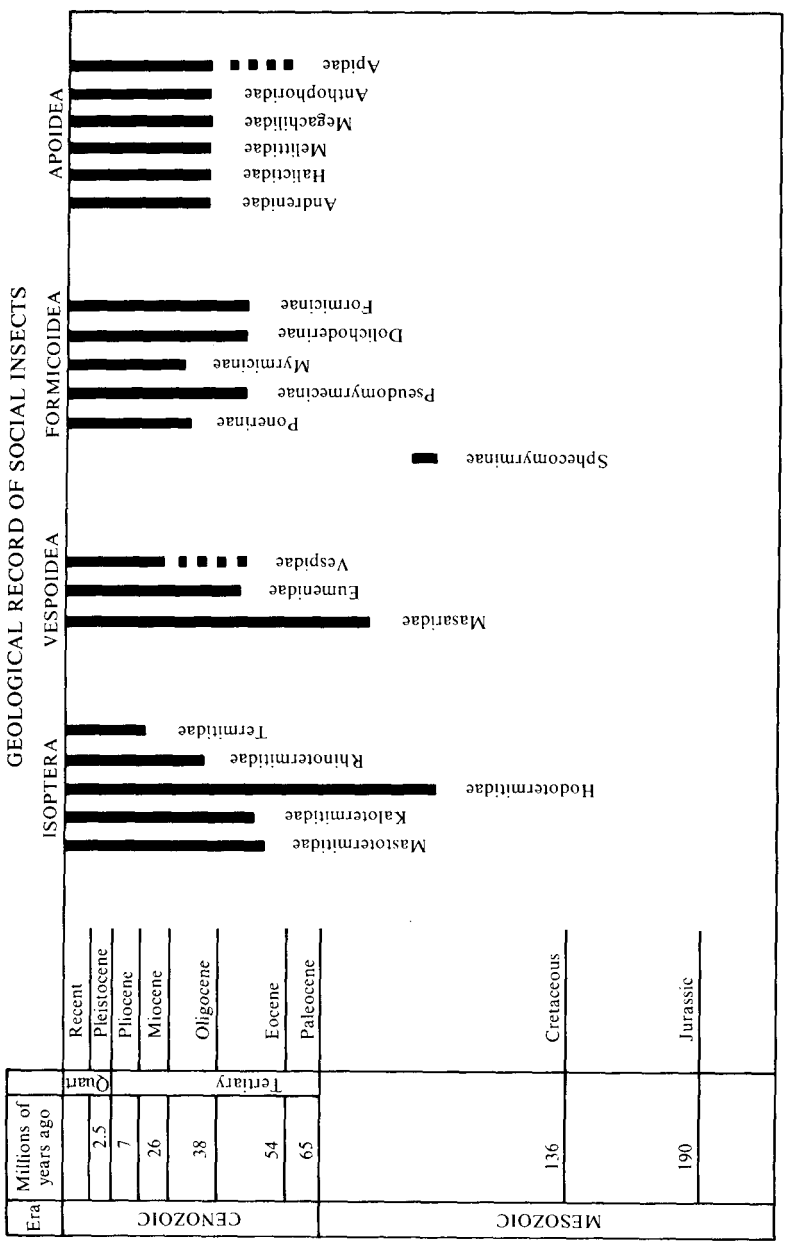

Figure 5. Geological time scale showing the distribution of twenty social insect families found in the fossil record. Dotted lines represent age extensions based on specimens of questionable taxonomic assignment.

ACKNOWLEDGEMENTS

This study was originally intended as a brief survey of the social insects in the fossil record but underwent rapid expansion shortly after its initiation. This is partly due to my burgeoning interest in the subject matter, partly due to the vast amount of material requiring my attention, and partly due to the stimulation and encouragement received from friends in the academic community at Harvard. It is to the following friends that I extend my thanks and appreciation: K. M. Horton, Paul Strother, Robert E. Silberglied, Kenneth Miyata, and N. E. Woodley. Special thanks are given to F. M. Carpenter for his continuous guidance and advice, for his patience as my photographic assistant; and most of all, deep appreciation is extended to him for providing the inspiration integral to the success of this study. The Royal Ontario Museum, Toronto, is gratefully acknowledged for the loan of the Eocene vespoid. In addition, partial financial support is acknowledged to National Science Foundation Grant DEB 78-09947 — F. M. Carpenter, principal investigator.

LITERATURE CITED

AHMAD, M.
1950. The phylogeny of termite genera based on imago-worker mandibles. Bull. Amer. Mus. Natur. Hist. **95**(2): 37–86.

ANDRÉ, E.
1895. Notice sur les fossiles de l'ambre de la Baltique et déscription de deux espèces nouvelles. Bull. Soc. Ent. Fr. **20:** 80–84.

BEQUAERT, J.
1930. On the generic and subgeneric divisions of the Vespinae (Hymenoptera). Bull. Brooklyn Ent. Soc. **25**(2): 70.

BROTHERS, D. J.
1975. Phylogeny and classification of the aculeate Hymenoptera with special reference to the Mutillidae. U. Kans. Sci. Bull **50:** 483 pp.

BROWN, W. L.
1973. A comparison of the Hylean and Congo-West African rain forest and faunas. *In* Meggers, B. J., Ayerson, E. S. and Duckworth, W. D. (eds.), Tropical Forest Ecosystems in Africa and South America: A Comparative Review, pp. 161–185. Smithsonian Institution Press, Washington, D. C.

BRUES, C. T.
1936. Evidences of insect activity preserved in fossil wood. J. Paleont. **10**(7): 637–643.

CARPENTER, F. M.
1929. A fossil ant from the Lower Eocene (Wilcox) of Tennessee. J. Wash. Acad. Sci. **19**(14): 300–301.
1930. The fossil ants of North America. Bull. Mus. Comp. Zool. Harv. **70**(1): 1–66.

CLEVELAND, L. R.
1934. The wood-feeding roach *Cryptocercus,* its protozoa, and the symbiosis between protozoa and roach. Mem. Amer. Acad. Arts Sci. **17**(2): 309–327.

COCKERELL, T. D. A.
1906. Fossil Hymenoptera from Florissant, Colorado. Bull. Mus. Comp. Zool. **50:** 55.
1909a. New fossil insects from Florissant, Colorado. Ann. Ent. Soc. Amer. **2:** 252.
1909b. Description of Hymenoptera from Baltic Amber. Schrift. Physik.-okon. Ges. **50:** 1–25.
1909c. Some European fossil bees. Entomologist **42:** 313–317.
1913. Genera *Parotermes* and *Hodotermes.* Ent. News **24**(1): 6–8.
1914. Miocene fossil insects. Proc. Acad. Natur. Sci. Philadelphia **66:** 638–648.
1915. British fossil insects. Proc. U. S. Nat. Mus. **49:** 469–499.
1920. Fossil arthropods in the British Museum I. Ann. Mag. Natur. Hist. **9** (5): 273–279.
1921a. Fossil arthropods in the British Museum V. Ann. Mag. Natur. Hist. **9**(7): 20.
1921b. Fossil arthropods in the British Museum VII. Ann. Mag. Natur. Hist. **9**(8): 545.
1921c. Some Eocene insects from Colorado and Wyoming. Proc. U. S. Nat. Mus. **59:** 29–39.
1923a. Fossil insects from the Eocene of Texas. Amer. J. Sci. **5:** 397–399.
1923b. The earliest known ponerine ant. Entomologist **56**(718): 51–52.
1927. Fossil insects from the Miocene of Colorado. Ann. Mag. Natur. Hist. **19:** 161–166.

DLUSSKY, G. M.
1975. *In* Rasnitsyn, A. P., Hymenoptera Apocrita of the Mesozoic. Trans. Paleont. Inst. **147:** 115–121. (Russian)

DONISTHORPE, H.
1920. British Oligocene ants. Ann. Mag. Natur. Hist. (5)**31:** 81–94.

EMERSON, A. E.
1955. Geographical origins and dispersions of termite genera. Fieldiana, Zool. **37:** 465–521.
1965. A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. Amer. Mus. Novit. no. **2236:** 1–46.
1967. Cretaceous insects from Labrador. 3. New genus and species of termite (Isoptera: Hodotermitidae). Psyche **74**(7): 276–289.
1968. A revision of the fossil genus *Ulmeriella* (Isoptera, Hodotermitidae, Hodotermitinae). Amer. Mus. Novit. no. **2332:** 1–22.

1969. A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). Amer. Mus. Novit. no. **2359:** 1–57.

1971. Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated flagellata (protozoa) and the Staphylinidae (Coleoptera). Bull. Amer. Mus. Natur. Hist. **146**(3): 247–298.

EMERSON, A. E. AND K. KRISHNA

1975. The termite family Serritermitidae (Isoptera). Amer. Mus. Novit. no. **2570:** 1–31.

EMERY, C.

1891. Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Universita di Bologna. Mem. R. Accad. Sci. Ist. Bologna (5)**1:** 141–165.

EVANS, H. E.

1966. The Comparative Ethology and Evolution of the Sandwasps. Harvard Univ. Press, Cambridge, Mass. 526 pp.

1969. Three new Cretaceous aculeate wasps (Hymenoptera). Psyche **76**(3): 251–261.

1973. Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). Psyche **80**(3): 166–178.

FUJIYAMA, I.

1970. Fossil insects from the Chôjabaru Formation, Iki Island, Japan. Mem. Nat. Sci. Mus. Tokyo **3:** 65–74.

GLICK, P. A.

1933. The distribution of insects, spiders, and mites in the air. Tech. Bull. U.S.D.A. **673:** 1–60.

HAMILTON, W. D.

1964. The genetical theory of social behavior, I, II. J. Theor. Biol. **7**(1): 1–52.

1978. Evolution and diversity under bark. Unpublished manuscript.

HEER, O.

1849. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien II. Neue Denkschr. Allg. Schweiz. Ges. Naturw. **2:** 1–264.

1856. Ueber die fossilen Insekten von Aix in der Provence. Viertl. Natur. Ges. Zurich **1:** 1–40.

1867. Fossile Hymenopteren aus Oeningen und Radoboj. Neue Denkschr. Allg. Schweiz. Ges. Naturw. **22**(4): 1–42.

1867. Fossil Hymenoptera. Neue Denkschr. Schweiz. Ges. Mem. **22:** 6.

HICKEY, L. J. AND J. A. DOYLE

1977. Early Cretaceous fossil evidence for angiosperm evolution. Bot. Rev. **43**(1): 1–104.

HILL, G. F.

1925. Notes on *Mastotermes darwiniensis* Froggatt (Isoptera). Proc. R. Soc. Victoria **37**(1): 119–124.

IMMS, A. D.

1919. On the structure and biology of *Archotermopsis,* together with descriptions of new species of intestinal protozoa, in general observations on the Isoptera. Phil. Trans. R. Soc. Lond. Ser. B, **209:** 75–180.

KELNER-PILLAULT, S.
1974. État d'évolution des apides de l'ambre balte. Ann. Soc. Ent. Fr. (N.S.) **10**(3): 623–634.
MANNING, F. J.
1952. Recent and fossil honey bees: some aspects of their cytology, phylogeny and evolution. Proc. Linn. Soc. Lond. **163**(1): 3–8.
MAYR, G.
1868. Die Ameisen des baltischen Bernsteins. Schrift. Physik.-ökon. Ges. **1**: 1–102.
MCKITTRICK, F. A.
1965. A contribution to the understanding of cockroach-termite affinities. Ann. Ent. Soc. Amer. **58**(1): 18–22.
MEUNIER, F.
1915. Ueber einige fossil Insekten aus den Braunkahlen Schichten von Rott. Z. Geol. Ges. **67**: 205–230.
1917. Sur quelques insectes de l'Aquitanien de Rott. Verh. K. Akad. Wet. **20**(1): 1–17.
1923. Sur quelques nouveaux insectes de lignites oligocenes de Rott, Siebengebirge. Verh. K. Akad. Wet. Proc. **26**: 605–612.
MICHENER, C. D.
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Natur. Hist. **82**(6): 157–225.
1962. Biological observations on the primitively social bees of the genus *Allodapula* in the Australian region (Hymenoptera, Xylocopinae). Insectes Sociaux **9**(4): 355–373.
1974. The Social Behavior of the Bees, A Comparative Study. Harvard Univ. Press, Cambridge, Mass. 404 pp.
NAORA, N.
1933. Notes on some fossil insects from East Asiatic continent, with descriptions of three new species. Ent. World **1**: 208–219.
PIERCE, W. D.
1958. Fossil arthropods of California, 21. Termites from Calico Mountain nodules. Bull. S. Calif. Acad. Sci. **57**: 13–24.
PITON, L.
1940. Paléontologie du gisement Éocène de Ménat. Thesis Fac. Sci., U. Clermont. 26 pp.
PITON, L. AND N. THEOBALD
1935. La faune entomologique des gisements Mio-Pliocenes du Massif central. Rev. Sci. Nat. d'Auvergne **2**: 1–40.
POPOV, V. V.
1933. Two new fossil ants from Caucasus. Trans. Inst. Paléo. Zool. Akad. Sci. USSR **2**: 17–21. (Russian)
PONGRACZ,
1928. Die fossilen Insekten von Ungarn. Ann. Mus. Nat. Hung. **25**: 166.
RASNITSYN, A. P.
1964. New Triassic Hymenoptera from Middle Asia. Paleont. J. **1964**: 87–96. (Russian)

1975. Hymenoptera Apocrita of Mesozoic. Trans. Paleont. Inst. **147:** 1–132. (Russian)
1977. New Jurassic and Cretaceous hymenopterans of Asia. Paleont. J. **1977:** 98–108 (Russian)

REGAL, P. J.
1977. Ecology and evolution of flowering plant dominance. Science **196**(4290): 622–629.

REID, G. M. AND M. E. J. CHANDLER
1933. The London Clay Flora. Brit. Mus. (Natur. Hist.) Lond. 561 pp.

RICHARDS, O. W.
1953. The Social Insects. Harper Torchbooks, New York. 219 pp.
1971. The biology of the social wasps (Hymenoptera: Vespidae). Biol. Rev. **46:** 483–528.

RIEK, E. F.
1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. Austr. J. Zool. **3**(4): 654–691.
1970. *In* The Insects of Australia. (CSIRO), Melbourne Univ. Press. 1029 pp.

SCUDDER, S. H.
1877. The insects of the Tertiary beds at Quesnel. Rep. Prog. Geol. Surv. Canada. 15 pp.
1878. The fossil insects of the Green River shales. Bull. U. S. Geol. Surv. Geogr. Terr. **4:** 747–776.
1890. The Tertiary insects of North America. Rep. U.S. Geol. Surv. **13:** 1–734.

SHAROV, A. G.
1957. First discovery of a Cretaceous stinging Hymenopteran (Aculeata). DAN **112**(5): 943–944. (Russian)
1962. OSNOVY. *In* The Principles of Paleontology. B. B. Rohdendorf, ed., p. 356. (Russian)

SIMBERLOFF, D. S. AND E. O. WILSON
1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology **50**(2): 278–296.

SIMPSON, G. G.
1952. Probabilities of dispersal in geologic time. Bull. Amer. Mus. Natur. Hist. **99**(3): 163–188.

SNYDER, T. E.
1949. Catalogue of the termites (Isoptera) of the world. Smithsonian Misc. Collns. **112:** 1–490.
1960. Fossil termites from the Tertiary amber of Chiapas, Mexico. J. Paleont. **34**(3): 493–494.

SOIKA, G.
1936. Caratteri del genre *Nortonia* Sauss. e descrizione di due nuove specie. Annali Mus. Civ. Stor. Nat. Giacomo Doria, **1936:** 268.

SPRADBERY, J. P.
1973. Wasps, an Account of the Biology and Natural History of Solitary and Social Wasps. Univ. Washington Press, Seattle. 408 pp.

STATZ, G.
1936. Ueber alte und neue fossile Hymenopteren—funde aus den tertiären Ablagerungen von Rott aus Siebengebirge. Decheniana **93:** 280–282.
STEBBINS, G. L.
1970. Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. Ann. Rev. Ecol. Syst. **I:** 307–326.
TAYLOR, R. W.
1978. *Nothomyrmecia macrops:* A living-fossil ant rediscovered. Science **201:** 979–985.
THEOBALD, N.
1937a. Les insectes fossiles des terrains Oligocènes de France. Bull. Soc. Sci. Nancy **2:** 1–467.
1937b. Note complémentaire sur les insectes fossiles Oligocènes des gypses d'Aix-en-Provence. Bull. Soc. Sci. Nancy **6:** 157–178.
TIFFNEY, B. H.
1977. Contributions to a monograph of the fruit and seed flora of the Brandon lignite. Ph.D. thesis, Dept. of Biology, Harvard Univ., Cambridge, Mass.
TILLYARD, R. J.
1926. The insects of Australia and New Zealand. Angus and Robertson, Sidney. 560 pp.
1936. Are termites descended from true cockroaches? Nature **137**(3468): 655.
TIMON-DAVID, J.
1944. Insectes fossiles de l'Oligocène inférieur des Camoins. Bull. Soc. Ent. Fr. **49:** 41.
VIANA, M. J. AND J. A. HAEDO-ROSSI
1957. Primer hallazgo en el hemisferio sur de Formicidae extinguidos y catalogo mundial de los Formicidae fosiles. Amighiniana **1**(1–2): 108–113.
WASMANN, E.
1929. Die Bernstein Paussiden und die Stammesgeschichte der Paussiden. 10th Cong. Intl. Zool., pp. 1497–1515.
WHEELER, W. M.
1914. The ants of the Baltic Amber. Schrift. Physik.-ökon. Ges. **55:** 1–142.
1928. The Social Insects. Harcourt, Brace, and Co., New York. 378 pp.
1929. The identity of the ant genera *Gesomyrmex* Mayr. Psyche **36**(1): 1–12.
WILLE, A.
1959. A new fossil stingless bee (Meliponini) from the amber of Chiapas, Mexico. J. Paleont. **33**(5): 849–852.
WILSON, E. O.
1955. A monographic revision of the ant genus *Lasius*. Bull. Mus. Comp. Zool. **113:** 1–201.
1971. The Insect Societies. Belknap Press of Harvard Univ. Press, Cambridge, Mass. 548 pp.
WILSON, E. O. AND R. W. TAYLOR
1964. A fossil ant colony: new evidence for social antiquity. Psyche **71**(2): 93–103.

WILSON, E. O., F. M. CARPENTER AND W. L. BROWN.
1967. The first Mesozoic ants, with the description of a new subfamily. Psyche **74**(1): 1–19.
WILSON, M. V. H.
1977. New records of insect families from the freshwater Middle Eocene of British Columbia. Can. J. Earth Sci. **14**(5): 1139–1155.
ZALESSKY, G. M.
1949. A new Tertiary ant. Soviet Geol. no. **40:** 50–54.
ZEUNER, F. E.
1939. Fossil Orthoptera Ensifera. Brit. Mus. (Natur. Hist.). 321 pp.
1944. Fossil bees. Brit. Bee-Keep. Assoc. Lond. **1944:** 10.
1951. A discussion of time-rates in evolution. Proc. Linn. Soc. Lond. **162:** 124–130.
ZEUNER, F. E. AND F. J. MANNING
1976. A monograph on fossil bees (Hymenoptera: Apoidea). Bull. Brit. Mus. (Natur. Hist.) **27**(3): 151–268.